

THE MACROBENTHOS OF BRAMBLE BAY, MORETON BAY, QUEENSLAND

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ABSTRACT

As part of a study of the possible effects of enlarging Brisbane Airport upon the biota of adjacent areas, the macro-benthos of Bramble Bay was investigated. Sites at *c.* 1 km apart were sampled in duplicate with an 0.1 m² van Veen grab and sieved through 1 mm mesh. The data gave two three-dimensional matrices; of *ca* 190 spp × 27 sites × 7 seasons (at three month intervals) and of *ca* 190 spp × 48 sites × 2 years respectively.

The number of species is roughly half that from a current survey of Middle Banks and roughly half that from a past study near Peel Island, both in Moreton Bay.

Analysis of the 3D matrices followed different patterns from those of Stephenson, Williams and Cook (1974), and these are detailed. They involved transformations using $\log(n + 1)$; also the species were standardized by totals prior to species classification. Data were scanned for outstandingly large values, and interactions of sites and times were explored via times classifications within site-groups.

Site classifications gave topographically coherent groups which generally followed an onshore-offshore sequence. The onshore sites, those most likely to be effected by airport construction, are characterized by *Spisula* and *Xenophthalmus* and have the highest populations but the lowest Shannon diversities of those investigated. The 48 sites data showed a site-group in proximity to the outflow of the Brisbane River.

Season classifications showed scarcely any grouping of similar seasons from two different years but instead groups of species persisted for *c.* 6-9 months and were then replaced by other groups. These temporal changes may be related to variations in runoff from land drainage and are most obvious in the area closest to the Brisbane River outflow.

Changes with time occur in almost all species. The magnitude of the time-changes suggests that 'base-line' studies for environmental impact statements in comparable situations (shallow water with some river influence) should involve extensive chronological replication. Prediction of the effects of airport construction would have been hazardous on the basis of present data because of other human activities in the area. A catastrophic flood ended the present study, caused unpredicted changes in the biota, and its effects will be described in a later paper.

This investigation was sponsored by the Australian Department of Housing and Construction and by the Queensland Department of the Coordinator General, and is part of a study of the possible effects of reclamation of an area east of the present Brisbane Airport. This would destroy mangroves, partly fill certain tidal creeks, and alter drainage patterns into the study area. It was hoped that a 'before' study of the macrobenthos of the area would lead to predictions of 'after' effects.

A relatively small area of Bramble Bay was sampled for macrobenthos at three-month in-

tervals and a larger area was sampled on successive Septembers. Experience gained at Peel Island in Moreton Bay by Stephenson, Williams and Cook (1974) suggested that a prolonged investigation might be required and the present work was planned to extend for an initial two years. An extreme flood in January 1974 caused dramatic changes in the biota and these will be considered in a later paper.

The data form two separate three dimensional groups: I of *c.* 190 species × 27 sites × 7 seasons, and II of *c.* 190 species × 48 sites × 2 years. To

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analyse data of this complexity requires numerical methods; present methods follow immediately upon the techniques of Williams and Stephenson (1973) and Stephenson, Williams and Cook (1974). They also follow up on the M.Sc. thesis of Raphael (1974) which dealt with seasonal data to March 1973 and this should be consulted for many relevant details e.g. sediment analyses, winds, rainfall. The present study involves three more seasons and more derivations from the data, and modifies certain aspects of the methods and conclusions.

SAMPLING AREA AND SAMPLING DETAILS

Moreton Bay has been described by Stephenson, Williams and Lance (1970), Maxwell (1970) and Newell (1971). The relevant portion is shown in Fig. 1 and the study area in Fig. 2.

Difficulties were encountered in selecting sampling sites and sampling times. Results obtained by Stephenson, Williams and Cook (1974) suggested that for one area of Moreton Bay it would have been desirable to have intersite distances of c. 0.25 km, to obtain quintuplicate catches of 0.1 m² at

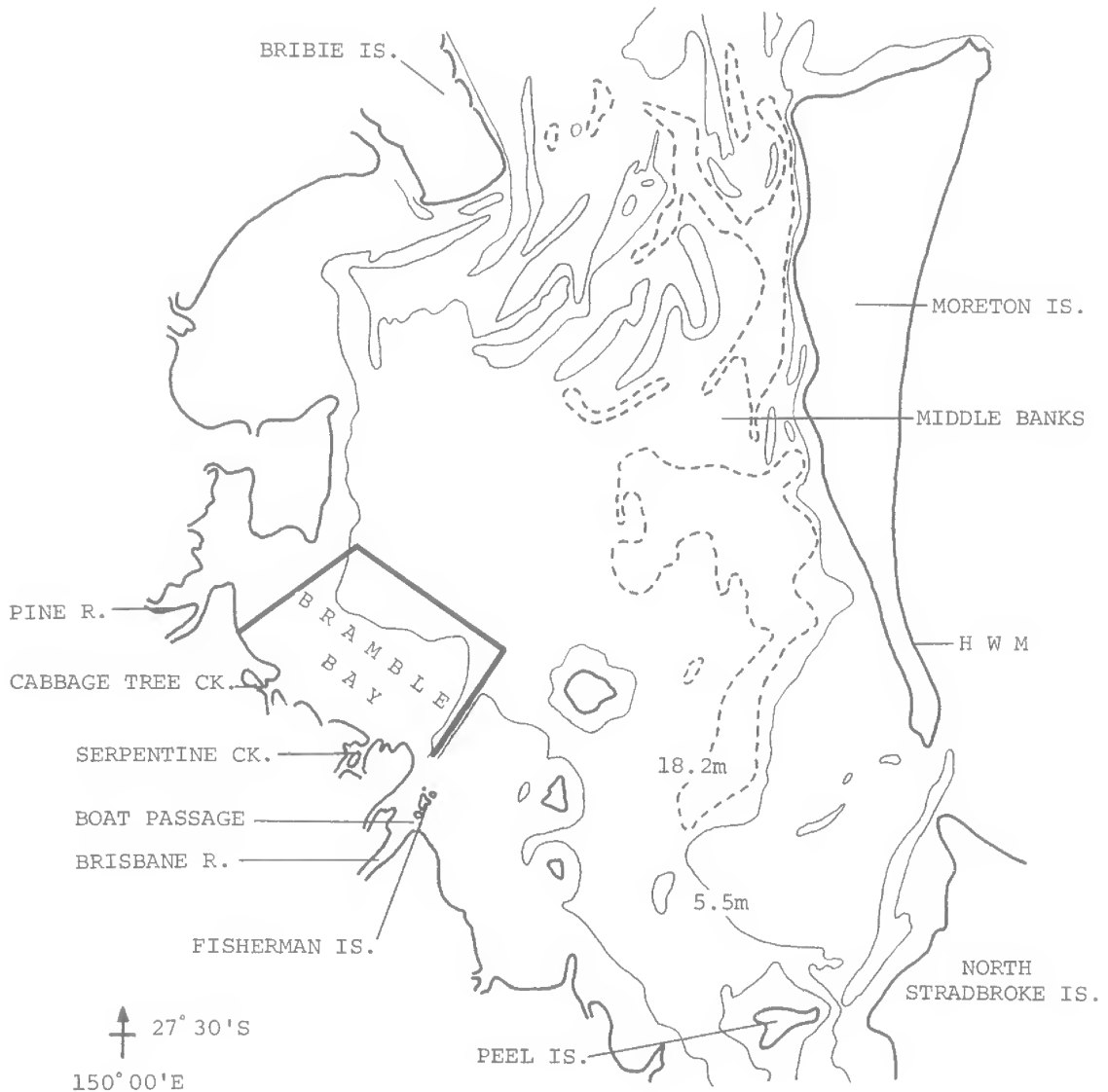


FIG. 1: Moreton Bay showing localities mentioned in text. Thick line high water mark, thin line 5.5 m (3 fm), broken line 18.2 m (10 fm). Very heavy line encloses sampling area.

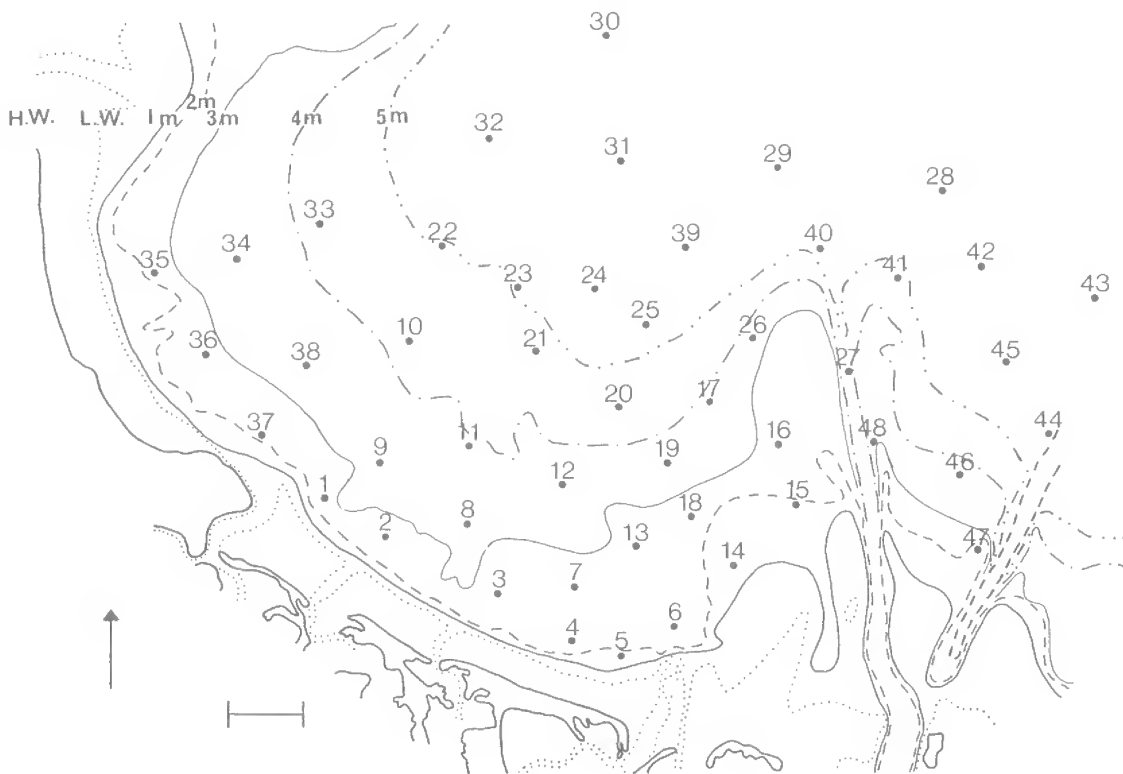


FIG. 2: Bramble Bay, with sampling sites and depth contours. Scale line = 1 km.

each site, and to sample at three-monthly intervals. Sampling at this frequency from the wide area of interest required relatively widely spaced sites and less replication of catches.

An initial trial was conducted with sites ca 1 km apart and with duplicate catches obtained by an 0.1 m² van Veen grab. This revealed clear patterns of species-groups within site-groups, and was adopted for subsequent sampling. For the three-month sampling a tolerably restricted study area was selected (sites 1–27) and this gave the series I data. The results suggested that less frequent studies of a wider area would be desirable and hence sites 1–48 were sampled annually—this gave the series II data. The latter were obtained in September because this was the season of highest populations in the previous study (Stephenson, Williams and Cook 1974).

Raphael (1974) should be consulted for the source of the depth contours on Fig. 2 (these differ from those of published charts) and for such data as exist on tides, winds and temperatures in the area. There are no worthwhile data on salinities but dilution effects are available indirectly from records of rainfall and from overflow discharges over a weir

on the Brisbane River. Details are given in Raphael (1974), and generalities are included in the present paper.

Information on sediments is contained in Maxwell (1970) but additional data were obtained during the present survey.

Each sample, comprising two catches from an 0.1 m² van Veen grab, was wet sieved on board through a final aperture of 1 mm. The residue was carefully examined for small specimens, particularly of gastropods and bivalves; only if these were present the sievings were preserved and the biota sorted at base.

SEDIMENTS

Sediments were sampled by selecting an aliquot of the grab contents, with precautions against loss of biota. For series I, sediment samples were collected thrice (June 1972, Dec. 1972, June 1973) and for series II, at each September.

After removal of organic matter by sodium hypochlorite solution, proportions of particle sizes were determined by wet sieving. Sieve sizes were (in mm): 2.00, 1.00, 0.50, 0.25, 0.125 and 0.063 and

the corresponding fractions are described as: gravel (= shell grit), very coarse sand, coarse sand, medium sand, fine sand and very fine sand respectively. The fraction not retained by the 0.063 mm sieve is referred to as mud.

Throughout there were considerable and apparently random variations between successive samples at a given site; these are believed due to the hand selection of samples from the grab. The upper part of the sample was generally coarser than the lower, and an excess of either would explain the results obtained.

The percentages of each sediment fraction at a given site were averaged and patterns were sought. The most meaningful are based on gradings of the percentages of mud, and of very coarse sand plus gravel respectively. The mud gradings adopted were: high $>75\%$, medium 50–75%, and low $<50\%$, and results are shown in Fig. 3. The coarse sediment gradings based on breaks in the data were: high $>13\%$, medium 7–11%, and low $<7\%$, results are shown in Fig. 4.

The mud distribution shows two tendencies: increase of muddiness with depth, and shorewards

extension of the more muddy areas opposite and slightly west of the main sources of land drainage. The latter are apparent off the Brisbane River and Cabbage Tree Creek. Opposite Serpentine Creek the effect is more localised and only the medium mud zone is involved.

The distribution of the coarser sediments presents an irregular pattern. There tends to be less coarse sediment in the offshore sites, and there are patches, generally isolated, with high content of coarse sediment. The coarse fractions mostly comprise dead bivalve shells and these areas of concentration presumably relate more to biotic distributions in the past than to hydrographic patterns in the present. It is of interest that dredging of shell grit for commercial purposes occurs in the area, but is shoreward of the main concentrations of coarse sediment (see Raphael 1974, fig. 4).

BIOTIC DATA

IDENTIFICATIONS: These were made in part by comparison with reference collections from previously published benthic studies in Moreton Bay



FIG. 3: Distribution of mud in sampled area. High proportion (mean % >75), coarse stipple; medium (50–75%), medium stipple; and low ($<50\%$), fine stipple. Scale line = 1 km.



FIG. 4: Distribution of coarse sediments (very coarse sand plus gravel = shell grit). High proportion (> 13%) coarse stipple, medium (7–11%) fine stipple, and low (~7%) medium stipple. Scale line = 1 km.

(Stephenson, Williams and Lance 1970; Stephenson, Williams and Cook 1974). Other reference collections (like the above housed in the Queensland Museum), were made by kind assistance from the following: Dr P. Hutchings, Australian Museum; polychaetes (terebellides and ampharettids); Mr B. M. Campbell, Queensland Museum; crabs: Dr C. R. Smalley, Zoology Department, University of Western Australia; alpheid: Dr W. F. Ponder, Australian Museum, Sydney; some gastropods: Dr A. N. Baker, National Museum, New Zealand; ophiuroids: Dr P. Mather, Queensland Museum; tunicates.

Numerous species have incomplete identifications and at least one taxon is known to be polyspecific; 'tunicate 1' comprises both *Molgula mollis* Herdman and *Cnemidocarpa floccosa* Sluiter.

NON-RECORDINGS: Grabs are inefficient collectors of penaeid prawns and benthic fish, and the few specimens obtained were not recorded.

Dead material was excluded as were empty tubes of polychaetes. *Chaetopterus variopedatus* was an

exception because intact specimens were not obtained; when the tubes appeared to have been inhabited recently, two tube-ends were recorded as one individual.

SPECIES OBTAINED

Raphael (1974) listed 182 species in her shorter survey; 4 additions were recorded in the three seasons of extension. In the comparable Peel Island survey of Stephenson, Williams and Cook (1974) roughly double this number was obtained (420 species) and a current study by Stephenson, Cook and Newlands (MS) records about 450 species from Middle Banks in Moreton Bay. Using a small grab in the Serpentine Creek area over five seasons of sampling, Stephenson and Campbell (in press) obtained ca 90 species, roughly half the present number.

Of the 182 species listed by Raphael (1974), polychaetes contained the largest number of species (39%) followed in decreasing order by bivalves (27%), arthropods (17%), echinoderms (6%), gast-

ropods (4%) and chordates (4%). These percentages are tolerably close to those made at Peel Island by Stephenson, Williams and Cook (1974).

Comparisons of individual species with those obtained in other local surveys are difficult due to incomplete identifications. The closest available comparison is to the Peel Island study, with 70 species known to be common.

METHODS OF ANALYSES

The account below excludes discussion of choice between most of the alternative methods which are available (see Clifford and Stephenson 1975). We have not followed the pioneer 3D study by Williams and Stephenson (1973) for reasons partly given in Stephenson, Williams and Cook (1974) and elaborated in the Discussion.

The data form two different three-dimensional matrices with dimensions s (species) $\times q$ (quadrats or sites) $\times t$ (times). The most convenient method of handling 3D data is to summate over one of the dimensions to produce three 2D matrices of $q \times t$, $s \times q$, and $s \times t$ respectively.

The $q \times t$ matrix as derived directly contains the summated numbers (N) of all species in each sample. Various other forms of $q \times t$ data are readily available. By reducing the recordings of species-in-samples to binary form we obtain the number of species (S) in each sample; this gives a simple measure of diversity per sample. More sophisticated measures are available and we have also used the Shannon diversity, (D) per sample ($N \log N - \sum_1^s n \log n$), and also per individual (H^1) expressing these to log base 10. For these four $q \times t$ matrices, recordings of all species are incorporated.

For the remaining analyses, there are advantages in reducing the number of species to consider. Raphael (1974) used different numbers of species for series I data (43) and series II data (51) basing the reductions upon ubiquity considerations. In the present case, in theory we used the same species for both analyses, employing the 81 species with recordings of 10 or more individuals in the total data (231 samples). In fact the species used in the two analyses differed slightly because a few species present in one series of data were absent in the other. The species considered are given in the Appendix. Where only a single species of a genus is there listed, it is referred to in the text by generic name only.

From the $s \times q$ matrix by classification we can obtain site-groups and species-groups on data summated (or averaged) over the times of sampling. From the $s \times t$ matrix by classification, we can

obtain time-groups and species-groups on data summated over all sites. These groupings, based on overall tendencies are of particular value in the context of the present study.

The techniques used in the present case following data reduction were: (a) prior to classification of entities (sites or times), transform recordings by using $\log_{10} (n + 1)$; (b) prior to classification of species, standardise by totals the transformed values; and (c) classify entities and species in both cases using Bray-Curtis dissimilarity measure and group-average sorting.

For easier interpretation of two-way tables, entities (i.e. sites or times) within entity-groups and species within species-groups were arranged by their sequential numbers.

Perusal of the two-way tables indicates that species-groups and their constituent species characterize certain entity groups by occurring there in greater numbers than elsewhere. In a few cases there is 'negative' characterizing by the occurrence of smaller numbers. As stated elsewhere (Stephenson and Dredge 1976) if these characterizations are effected purely by visual inspection of the data there are risks of subjectivity, while if we use statistical tests of the significance of differences these are open to criticism. Because data are near-optimally grouped we are not comparing random samples. As in the previous paper (Stephenson and Dredge 1976) we use the mechanics of certain statistical tests because they appear to follow closely the conclusions reached by visual inspection of the data. We avoid throughout use of the word 'significantly' and use instead 'noticeably' or 'outstandingly'.

Tests were at two levels, the first were for 'scanning' purposes and to determine whether or not entity-group means appeared different. (It should be noted that in the case of time-groups, each entity was taken as forming a group.) In general χ^2 tests were employed using 'raw' (untransformed) summated values. The test was extended below its legitimate limits of *c.* 5 per group (Sokal and Rohlf 1969, p. 565) because it is being used purely for indicative purposes.

When entity-groups appear different by χ^2 testing, there may still be such inter-group variation that the differences are not 'real', hence at a second level the more stringent *F* test was employed, with prior transformation of data using $\log_{10} (n + 1)$.

The results are expressed in terms of noticeability of difference, with HN the equivalent of < 0.01 probability and N of < 0.05 probability as these levels would be applied in usual significance testing. It should be stressed that the true noticeability will

be less than that ascribed because the data have been summated along one of the axes of the 3D matrix, and variation in that axis has been suppressed.

RESULTS

The series I and series II data are separately treated.

SERIES I (27 sites, 7 times)

QUADRATS \times TIMES DATA

The four matrices involving values of N , S , D and H^1 are conveniently approached by summations to give quadrat means and times means—these are given in Table 1. Heterogeneity in the data is of interest and variances of the tabulated means are also given in Table 1, together with the within quadrat and within times variances of N .

Populations (N values) and their variances are highest in quadrats 1, 4, 5, 6 and 14 and in times 5, 6 and 7. The high values and high variances are due to isolated extremely high values as follows: quadrat 1 times 6 and 7, $q4\ t6$, $q5\ t5$ and $t7$, $q6\ t6$ and $t7$, and $q14\ t1$ and $t6$. While these population values are 'patchy' there are clear hints of patterns in this patchiness: the high values are in the inshore sites and mostly in the later sampling periods.

Variances in N values in quadrats and in times are heavily biased by the above outstandingly large sample populations. Thus by excluding the above nine results (ranging from 991 to 4581) the overall variance is reduced by 98%. These high values also contribute largely to the variance interaction of quadrats and times which is 74% of the total variance in the N matrix.

Spearman rank correlation coefficients were derived for various pairs of the columns in Table 1 with results in Table 2.

The high positive correlation for quadrat values between N and D implies that diversities per individual are more meaningful than diversities per site. H^1 values are positively correlated with S , the number of species per site, and negatively correlated with the populations per site.

The correlations for times are not significant in any of the cases. It should be noted that the times interrelationships and quadrat interrelationships did not follow similar patterns. Thus in the times data S and D showed a high positive correlation and also N was positively and not negatively correlated with H^1 .

Considering the H^1 values, variances between sites (0.045) are much greater than the variances between times (0.003). All inshore sites give low H^1

TABLE 1: ANALYSIS OF $q \times t$ DATA

Means and variances of N ; means of S , of D and of H^1 in quadrats and in times. Variances of means are also given. All values rounded.

QUADRATS

Quadrat No.	Mean N	Variance N	Mean S	Mean D	Mean H^1
1	829	2842922	7	62	0.45
2	110	5044	9	52	0.51
3	145	5452	10	63	0.55
4	215	150166	10	61	0.46
5	1002	2660803	11	109	0.28
6	452	448781	12	92	0.44
7	28	135	15	31	1.07
8	61	3219	12	33	0.66
9	24	643	8	14	0.75
10	25	175	11	24	0.91
11	45	348	15	38	0.88
12	33	457	13	31	0.93
13	31	256	13	30	0.95
14	506	407509	10	36	0.48
15	33	333	12	25	0.84
16	43	525	15	42	1.02
17	47	907	10	26	0.62
18	53	536	13	40	0.78
19	66	4828	18	55	0.95
20	64	5166	12	38	0.73
21	82	5451	12	44	0.64
22	46	261	16	48	1.01
23	103	7356	16	81	0.83
24	87	1372	15	61	0.85
25	91	2412	14	61	0.69
26	38	1451	15	33	0.98
27	19	141	9	15	0.80
Overall mean	158.4		12.2	46.1	0.740
Variance of means	62169		7.67	511	0.045

TIMES

Time No.	Mean N	Variance N	Mean S	Mean D	Mean H^1
1	130	60565	14	53	0.69
2	102	16168	14	51	0.77
3	107	12646	16	66	0.80
4	53	922	9	30	0.63
5	199	767666	10	31	0.80
6	367	908480	13	57	0.76
7	150	115420	9	37	0.73
Variance of means	10495		7.81	193	0.003

TABLE 2: SPEARMAN RANK CORRELATION COEFFICIENTS FOR DATA IN COLUMNS OF TABLE 1. (H.S. = 0.01, N.S. = 0.05)

	<i>N</i> cf. <i>D</i>	<i>S</i> cf. <i>D</i>	<i>S</i> cf. <i>H</i> ¹	<i>N</i> cf. <i>H</i> ¹
Quadrat means	+0.86 (HS)	+0.11 (NS)	+0.66 (HS)	-0.77 (HS)
Times means	+0.25 (NS)	+0.79 (NS)	+0.38 (NS)	+0.23 (NS)

values (sites 1-6 and 14) and there is also a low H^1 value at time 4 (March 1973). This coincides with the lowest populations.

Further discussions of the $q \times t$ data are deferred pending analysis of the $s \times q$ and $s \times t$ matrices.

SPECIES \times QUADRATS DATA

SITE-GROUPS: The dendrogram of site-groupings (Fig. 5) shows a near trichotomy into three unequal groups, the largest group then giving two small and two larger groups. By accepting the above we derive a 7-site inshore group (*I*), a 7-site middle group (*M*) and an 8-site offshore group (*O*), plus five sites in three groups. These sites were allocated to one or another of the three main groups in the order of sites 16, 18, 27, 8 and 9 on the basis of Bray-Curtis comparisons of $\log(n+1)$ data with group means. The three revised groups are:

Inshore (*I*): sites 1, 2, 3, 4, 5, 6, 8, 9, 14.

Middle (*M*): sites 7, 10, 11, 13, 15, 16, 18, 19, 26, 27.

Offshore (*O*): sites 12, 17, 20, 21, 22, 23, 24, 25.

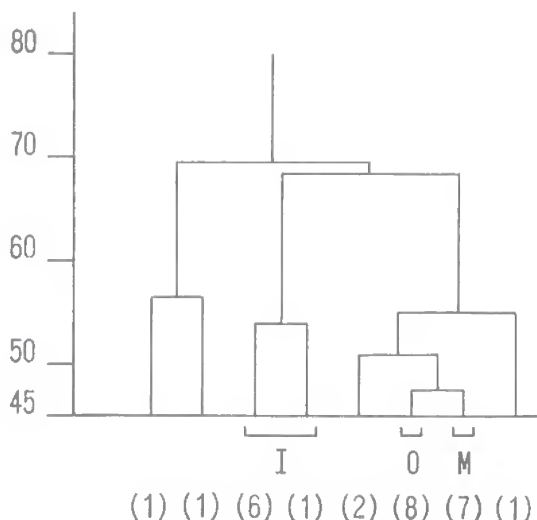


FIG. 5: Truncated dendrogram of classification of 27 sites by species; sites in each group at dendrogram base. *I* sites are inshore, *M* at middle depths and *O* offshore. Sites not in marked groups were re-allocated.

These groups make a coherent topographical picture (Fig. 6). Thus they conform to the extrinsic attribute of proximity; they are also the groups giving the maximum number of outstanding species (i.e. maximum conformity to intrinsic attributes).

SPECIES-GROUPS: The eleven groups originally accepted are shown by dendrogram in Fig. 7. They involved accepting lower dissimilarity levels within the larger groups.

F tests were employed (on transformed data) species by species to determine which had noticeably different values in the three site-groups. In several cases where using three groups failed to show differences one group was tested against the two others and differences were then noticeable. Species which conformed to these tests and those which do not are considered separately. The former comprise 53 of the 79 species in the analysis.

Species-groups with a majority of species conforming to the 3 site-groups: Five groups are involved and these with their constituent species are listed below: non-conforming species are in parenthesis. Site-group characterizations by these species-groups are also given.

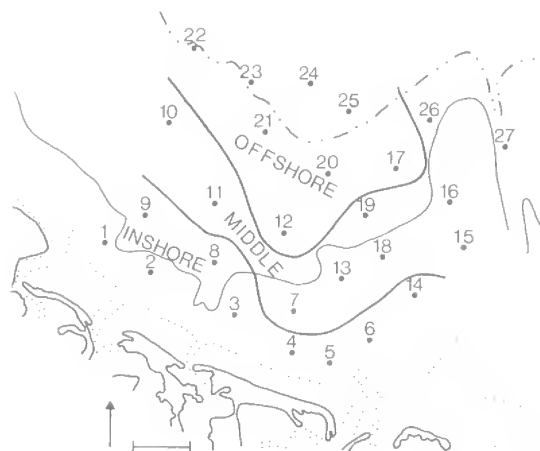


FIG. 6: Site-groups; 27 sites classified by species, after re-allocation of sites. Scale line = 1 km.

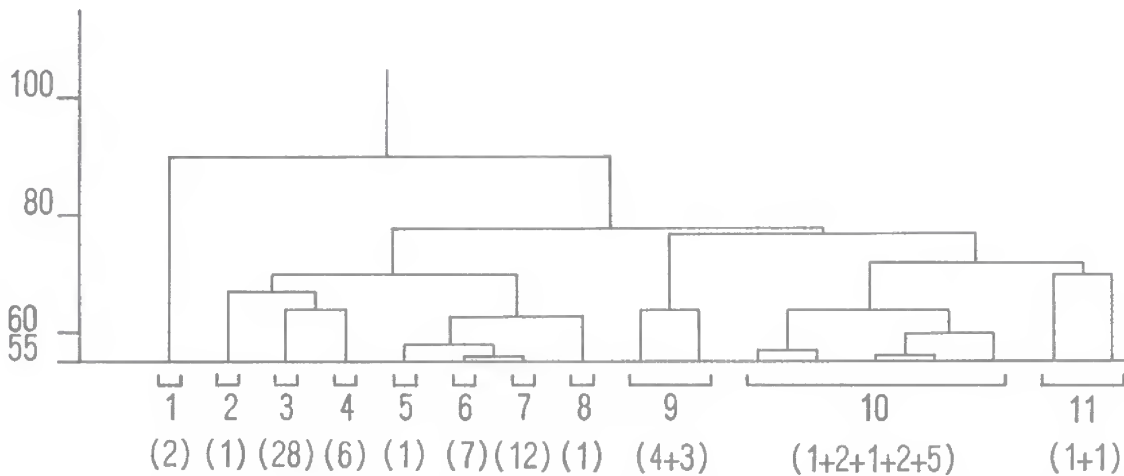


FIG. 7: Series I data; truncated dendrogram of classification of species by sites (species 35 and 75 with nil records, eliminated). At base the species-group numbers used in text, and in parenthesis the numbers of species in each.

Species-group 3: spp. 4, 6, 7, 8, 10, 12, 13, 14, 17, 19, 20, 21, 23, 25, 29, 30, 33, 37, 42, 45, 48, 53, 57, 58, 62, 66 (32, 47). Highest recordings (with minor exceptions) in offshore site-group, lowest in inshore group; designated 'offshore' species.

Species-group 5: sp. 26. Restricted to inshore site-group (and only in certain of these—see later).

Species-group 6: spp. 5, 18, 28, 50, 54, (41, 55). 'Middle' species, highest recordings middle site-group.

Species-group 7: spp. 1, 3, 9, 11, 15, 16, 24, 40, (31, 51, 65, 76). 'Inshore' species.

Species-group 8: spp. 22, 43, 46, 49, 59, 60, 61, 63, 68, 70, 73, 77 (79). 'Middle' species, differences from species-group 6 detailed below.

Summating gives 26 offshore, 17 middle, and 8 inshore species.

While the major site pattern is clearly that of the three main groups, perusal of the data revealed that there are smaller site-groups within them. Thus species 26 (species-group 5) occurs in high numbers in sites 1–4 with low numbers in sites 5–7 and is absent from the remainder. It is a 'sites 1–4' species. Similarly species 45, 47, 58 and 62 (of species-group 1) are a 'sites 21–25' species. These two groups of sites are on the western side of the samples area; 1–4 being western inshore and 21–25 western offshore.

The differences between species-groups 6 and 10 are that in the latter there are proportionally fewer specimens in the inshore site-group, and that the species are concentrated in sites 13, 16, 18, 19, 26, 27, i.e. in the eastern portion of the middle site-group.

Species-groups not conforming to the 3 site-groups: These comprise: group 1, spp. 2, 70; group

2, sp. 67; group 4, spp. 27, 34, 39, 52, 56, and 69; group 8, sp. 80; group 9, spp. 36, 38, 44, 64, 71, 74, 78; and group 11, spp. 72 and 81.

Only one of these species-groups characterizes an extensive and topographically coherent area. This is species-group 4 and all its contained species except one have HN conformity to sites 7–12, 14, 26 and 27. (Apart from one outstandingly large value, the remaining species, 27, also conforms at the HN level.) The area involved approximates to the middle site-group less the sites closest to the Brisbane River, and this general area appears as a discrete site-group in the series II data.

The remaining species-groups have little internal coherence and species are separately considered. Eight species are significantly concentrated at a single site and are designated 'patchy' species. The species with their sites of concentration in parenthesis are 2(14), 27(16), 36(16), 38(27), 44(16), 46(16), 64(16), and 78(16). Six of the eight species are concentrated at site 16.

For the remaining species, it is possible to divide the sites into two groups to obtain noticeably different results, but to do this involves site-groupings which approximate to random scatter throughout the sampled area. The species involved are: 31, 32, 51, 55, 67, 71, 72, 74, 76, 80, 81. These probably include some having pseudo-uniform distribution over the whole area (eg. 31, 32) and others present in too low numbers for patterns to show (eg. 71, 72, 74, 76, 80, 81).

FEATURES OF THE SITE-GROUPS: If the main site-groups are regarded as communities then there are three sets of data on these groups: species composition, sample characteristics from the $q \times t$

TABLE 3: SERIES I DATA (27 SITES); SPECIES \times SITES
A. MEAN NUMBER OF SPECIMENS/m²* OF MORE
ABUNDANT SPECIES (IN SPECIES-GROUPS) IN SITE-GROUPS

Species Group	Species, and code No.	Site-groups (sites in parenthesis)		
		I (1-6, 8, 9, 14)	M (7, 10, 11, 13, 15, 16, 18, 19, 26, 27)	O (12, 17, 20-25)
3	<i>Paratapes</i> , 4	1	16	158
	<i>Amphioplus</i> sp., 6	<1	3	20
	<i>A. lobatus</i> , 7	<1	5	29
	<i>Theora lata</i> , 8	<1	1	10
	<i>Amphitrite</i> , 10	3	6	11
6	<i>Anadara</i> , 5	3	29	6
	tunicate 1, 18	2	5	1
7	<i>Spisula</i> , 1	1347	1	0
	<i>Xenophthalmus</i> , 3	140	38	8
	<i>Terebellides</i> , 9	20	3	2
	<i>Pupa</i> , 11	15	0	0
	<i>Parcanassa</i> , 15	12	2	1
10	oyster 1, 22	0	3	1
	<i>Arca</i> sp. 1, 43	<1	2	<1

* Mean number of specimens per sample, converted to numbers/m² and rounded to nearest unit.

B. MEAN POPULATIONS AND MEAN INDIVIDUAL SHANNON
DIVERSITIES* IN SITE-GROUPS

	Site-groups		
	I	M	O
Mean N/m^2	1858	190	346
Mean H^1	0.51	0.92	0.78

* Meaned from values per sample of two 0.1 m² grab catches.

C. MEAN NUMBER OF SPECIMENS/m²* OF MORE
ABUNDANT SPECIES IN ALTERNATIVE SPECIFIED SITE-
GROUPS

Sites specified	Species, and code No.	Mean numbers/m ² in:	
		Sites specified	Remainder
1-4	<i>Ophelina</i> , 26	16	<1
21-25	<i>Amphioplus depressus</i> , 45	4	1
	<i>Leptomys</i> , 47	2	<1
22-25	tunicate 3, 19	7	1
	<i>Ophiactis</i> , 59	2	<1
7-12, 14, 26, 27	<i>Petaloproctus</i> , 34	2	<1
	<i>Edwardsia</i> , 39	2	<1

* Mean number of specimens per sample, converted to numbers/m² and rounded to nearest unit.

data, and abiotic features. The first is indicated in the 2-way coincidence table (Table 3A) in which only the most abundant species in each species-group are listed. More briefly the inshore group would be described as *Spisula-Xenophthalmus-Terebellides* community, the middle group as a *Xenophthalmus-Anadara-Paratapes* community and the outer group as a *Paratapes-Amphioplus lobatus* community.

Comparable data on the species which characterise alternative site-groupings are given in Table 3C. Data from the $q \times t$ matrices are given in Table 3B. They comprise mean values of N converted to individuals/m² and mean values of individual diversities (H^1). This table shows that the inshore community has the highest mean population but lowest individual diversity; the converse is true of the middle community.

Perusal of Figs. 3 and 6 shows that there is a partial relationship between site-groups and distribution of mud in the sediments. Thus there is near coincidence between the offshore site-group and the area of most muddy sediments, and broadly similar concentric patterns radiating from this area. There are also comparable shorewards protrusions of the medium mud sediments and the middle site-group.

The correspondence between site-groups and mud distribution breaks down in the eastern part of the sampled area. Moreover the eastern site-group does not coincide with the area of high concentration of coarse sediments (see Fig. 4).

There is a similar partial relationship between site-groups and depths. While in the western part of the area, the site-groups occupy different depths, this fails to apply to the eastern part. The simplest overall explanation is that a depth-sediment relationship holds in the western part of the area, but that this is obliterated in the eastern part by some effect of the Brisbane River.

SPECIES \times TIMES DATA

TIME-GROUPS: The dendrogram of time-groupings (Fig. 8) shows two biotically isolated times— t_4 (March 1973) and t_7 (Dec. 1973)—and at a lower level two more coherent groups of times 1, 2, 3, (June–Sept. 1972) and times 5, 6 (June–Sept. 1973) respectively. The acceptance of these groups is at a dissimilarity level of c. 0.25 while acceptance of the three major site-groups in Fig. 5 was at the level of ca 0.45. Clearly while the inter-times group heterogeneity is appreciable it is much less than the inter-site group heterogeneity.

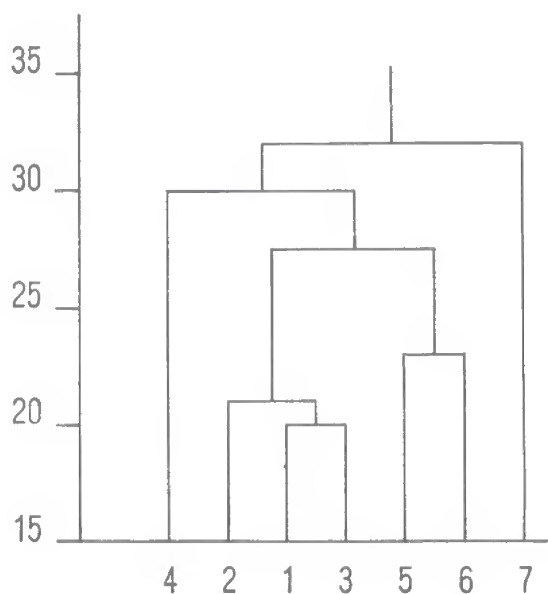


FIG. 8: Series I data; truncated dendrogram of classification of times by species.

If there had been a marked seasonality of the data, time-groupings such as 1, 5; 2, 4 and 3, 7 would have been expected. These did not occur.

SPECIES-GROUPS: The dendrogram gave very unequal groupings; it is not here given because none of the major species-groups were considered as satisfactory from a conceptual viewpoint. 'Satisfactory' species-groupings, as were obtained in the $s \times q$ analyses, are those in which entities (sites or times) are similarly characterized by the species in the group.

The computer-based analyses were replaced by visual and hand calculator analyses. They began by visual scanning the transformed recordings of a given species to select outstanding values. These are usually outstandingly high, in which case times of abundance are selected and times are positively characterized. Occasionally the outstanding values are low, times of scarcity are selected, and the characterization is negative.

The recordings of each species were then divided into two groups—the outstanding values and the remainder—and F tests were then performed on these two groups. Following this, species were grouped by their characterizations of times. Results are given in Table 4.

Table 4 shows that many species (35) positively characterized sequential time patterns, particularly

times 1–3 (14 spp.). Only six species showed seasonal re-occurrences of high recordings. The remaining species have been allocated to four groups as follows:

- (a) Distorted seasonal (positive)—2 spp. Here there is re-occurrence of high recordings to an approximate seasonal pattern. Because there were only four samplings per year and because advance or delay in seasonal peaks may well occur, these may be truly seasonal species.
- (b) Single time—9 positive spp., 6 negative spp. These are referred to later as 'time-patchy' species.
- (c) Nonsensical—9 spp. These had markedly different recordings throughout three sampling periods, and typically high, low and high, giving a 'saw-tooth' graph.
- (d) No times characterized—10 spp. In these there were no outstanding recordings and

TABLE 4: TIME-GROUPINGS CHARACTERISED BY SPECIES: SERIES I DATA

Times	Species characterization	
	Positive	Negative
Sequential		
1–3	4, 5, 9, 10, 18, 20, 24, 32, 37, 41, 42, 56, 57, 74	
2–3	28, 61, 74	60
5, 6	1, 7, 22, 26, 38, 69, 76, 81	
1–6	25, 50, 52	
1–4	4, 9	
2–4	48	
3, 4	29, 45, 64	
2–5	15	
6, 7	34, 43, 47	
Seasonal		
2, 6	12, 31, 49	
3, 7	27, 36, 54	
Distorted Seasonal		
1, 2, 6	2	
2, 5	16	
Single time		
1	67, 72	
2	19	
3	21, 59	
4		14, 33
6	71	
7	8, 39, 44	11, 23, 50, 52
Nonsensical	3, 16, 17, 30, 46, 51, 62, 68, 73	
No times characterized (Random)	53, 55, 63, 65, 66, 70, 77, 78, 79, 81	

testing raw values with χ^2 showed no noticeable difference from randomness. They are referred to below as random species.

The time-patchy and nonsensical species (24 in all) may either have rapid changes in populations or, more likely, result from a patchy microtopographical distribution. The random species are all low in the abundance hierarchy, and randomness is likely to be due to small recordings rather than truly stable ones.

FEATURES OF THE TIME-GROUPS: As with site-groups there are three sets of relevant data: species composition, sample characterisation from the $q \times t$ data, and possible abiotic 'explanations'.

The reduced 2-way coincidence (Table 5A) indicates the most important positively characterizing species of these time-groups, while Table 5B shows the population and individual diversity data.

In brief, times 1–3 are a period of *Paratapes*, *Anadara*, *Terebellides* and *Amphitrite*; there are no species positively characterising time 4 only; times 5 and 6 are a period of *Spisula* and *Amphioplus lobatus*; while time 7 is a period of *Theora lata*.

TABLE 5: SERIES I DATA (27 SITES); SPECIES \times TIMES
A. MEAN NUMBER OF SPECIMENS/m²* OF MORE ABUNDANT SPECIES IN GROUPS (FROM TABLE 4) IN TIME-GROUPS

Species, and code No.	Times			
	1–3	4	5, 6	7
<i>Paratapes</i> , 4	101	57	4	5
<i>Anadara</i> , 5	23	10	6	5
<i>Terebellides</i> , 9	17	7	1	1
<i>Amphitrite</i> , 10	11	5	3	2
tunicate 1, 18	5	1	1	1
<i>Spisula</i> , 1	127	28	1082	572
<i>Amphioplus lobatus</i> , 7	9	7	16	8
<i>Theora lata</i> , 8	1	0	0	20

* Mean number of specimens per sample, converted to numbers/m² and rounded to nearest unit.

B. MEAN POPULATIONS AND MEAN INDIVIDUAL SHANNON DIVERSITIES* IN TIME-GROUPS

	Times			
	1–3	4	5, 6	7
Mean N/m^2	563	265	1415	750
Mean H^1	0.75	0.63	0.78	0.73

* Measured from values per sample of two 0.1m² grab catches.

In terms of population density times 1–3 and 7 are about average, time 4 is outstandingly low and times 5 and 6 outstandingly high. Individual diversities are quasi-constant throughout except for a marked low in time 4.

Overall the most dissimilar time is time 4 (March 1973). Comparable studies near Peel Island in Moreton Bay by Stephenson, Williams and Cook (1974), revealed outstandingly low populations in their two March samplings. Moreover the lowest values were in March 1970 which followed a period of normal climate, instead of in March 1971 following the wettest summer (Dec.–Feb.) for 24 years. In the present case March 1972 follows a dry period.

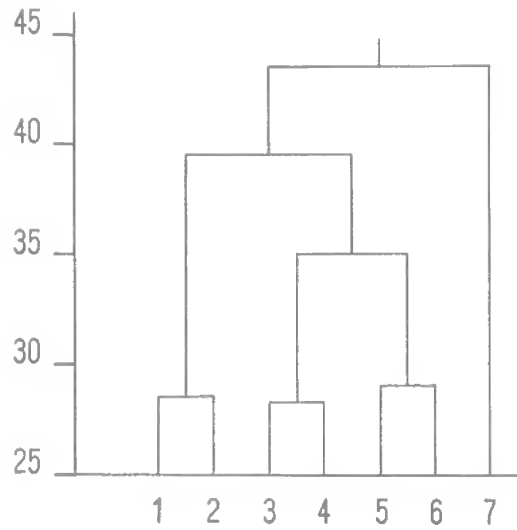
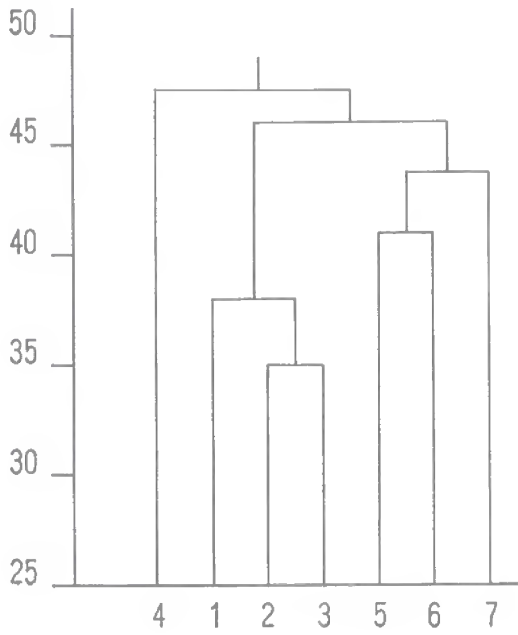
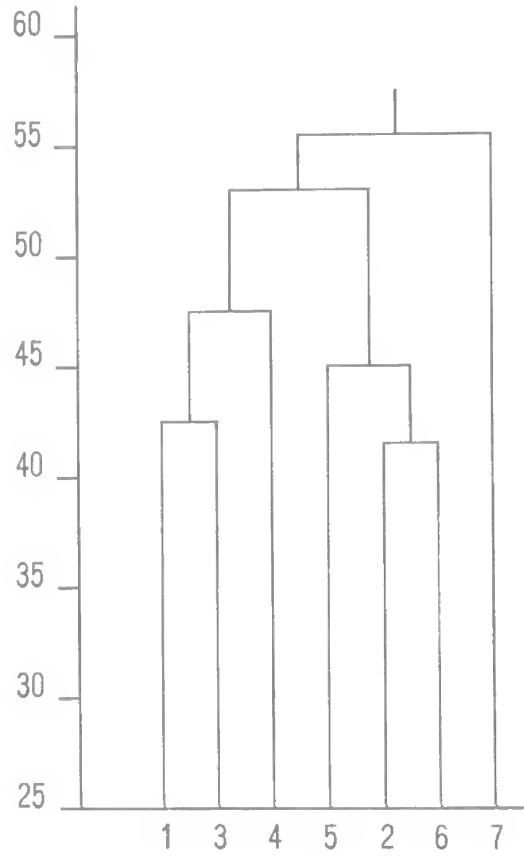
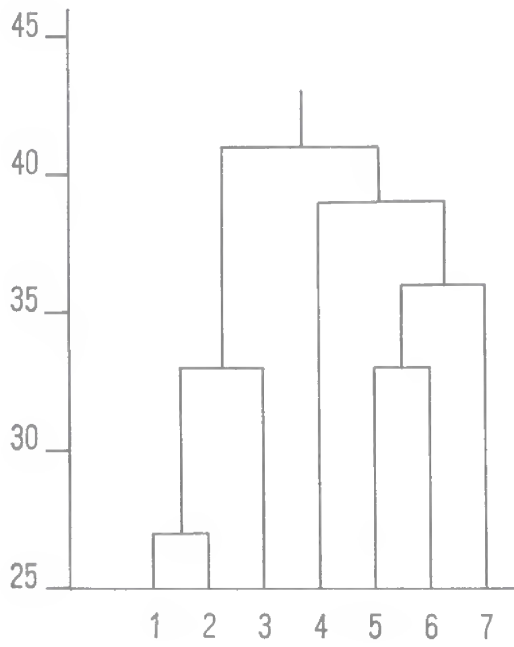
The effect of rainfall would be primarily by run-off from the Brisbane River, and data in Raphael (1974) show less than normal discharge in the Brisbane River for eight of the nine preceding months. Assuming that river run-off is the controlling factor then times 1–3 fall in a period of reduced run-off but one which follows a wetter period (Feb.–May 1972). Conversely times 5 and 6 fall in a period of approximately normal run-off but one following a drier period (June 1972–May 1973). On this basis the difference between times 3 and 7 (Dec. 1972 and Dec. 1973) reflects the low run-off preceding the former, and the approximately average run-off preceding the latter.

The only other continuous abiotic data of seeming relevance to the present situation are of air temperatures. There are no obvious relationships between these data and the time-groups.

FURTHER ANALYSES

Following the above analyses, two others suggested themselves. Both are concerned with shortcomings of the technique of converting a three-dimensional matrix into three two-dimensional ones.

EXTREME SPACE-TIME PATCHINESS: During summation across one of the axes of the matrix, variation along that axis is suppressed. Thus a high recording of a species in a site may be based upon uniformly high recordings in all times or may be based upon an extraordinarily high recording at a single time. Such a value could bias both the $q \times t$ and $s \times q$ analyses. A simple method was used to recognise species showing extreme 'space-time' patchiness by way of a single outstanding recording. The transformed data on each species (79 in all) was considered within its own $q \times t$ (27 \times 7) matrix. The F test was then applied comparing the largest recording with the remainder.



FIGS. 9-12: Series I data; dendrogram of classification of times by species.

FIG. 9: Inshore sites.

FIG. 10: Mid-eastern sites, nearest Brisbane River.

FIG. 11: Mid-western sites.

FIG. 12: Offshore sites.

To determine which results show extreme patchiness we must decide on a probability in relation to the F level. The lowest listed in tables is 0.001, and to accept this would give 73/79 extremely patchy species. Taking five times the F level at the 0.001 value gives the following 25 space-time patchy species: 2, 19, 22, 27, 34, 36, 38, 43, 44, 50, 59, 60, 61, 63, 64, 65, 68, 69, 70, 71, 72, 73, 74, 77, 78, 81.

The species previously judged site-patchy are: 2, 27, 36, 38, 44, 46, 64, 78, and 7/8 of these are in the above list. Of the 15 species previously judged time-patchy only six appear on the above list: 19, 44, 50, 59, 71, 72. It is evident that the present method does have cautionary value, particularly regarding space-patchiness.

The places and times of the space-time patchiness give concentrations as follows: *quadrats* 11, 13, 16, 18, and 19 which are all in the middle site-group and mostly on its eastern side, and *times* 3, 5, 6, 7; these are mostly towards the end of the sampling period.

INTERACTIONS BETWEEN SPACE AND TIME: The usual calculations of variance interaction essayed on a species by species basis, showed that most of the interaction was due to the few, usually single, outstandingly large values as considered above.

Further and more directly meaningful analyses involving interactions were then undertaken and for two reasons: (i) the main heterogeneity is between sites; by operating within site-groups it seems possible that times-groups would be more coherent and (ii) within different site-groups one might expect differences in time-groupings. If the previous argument that variable run-off from the Brisbane River explains some of the results is correct, then the greatest time-dissimilarities should occur in the sites adjacent to it.

The three original site-groups were converted to four by arbitrary division of the middle one and by transfer of one site (12) to the group suggested by its topography. This gave:

Inshore: sites 1-6, 8, 9, 14.

Middle eastern (nearest river): sites 15, 16, 18, 26, 27.

Middle western: sites 7, 10-13, 19.

Offshore: sites 12, 16-18, 20-25.

The four dendrograms of time-groupings within these site-groups are given in Figs. 9 to 12.

The mean percentages dissimilarity at which times separate as individual entities are as follows: inshore 32.6, mid-eastern 44.9, mid-western 39.9, outer 30.5. As expected the site-group nearest the river shows the greatest time heterogeneity. Possibly the river influence extends to the mid-western

region; this shows greater time-heterogeneity than the inshore site-group.

The inshore group shows division by years into time 1-3 and 4-7, and in the midwest there is a somewhat similar picture (times 1-3 and 5-7). The mid-east has a broadly annual picture, upset by a seasonal linkage of times 2 and 6. The offshore area differs from the remainder in having three groupings of successive times, viz: times 1, 2 and 3; 4 and 5; 6.

Species-groupings were examined in each of the above cases. Those produced by the classificatory programme failed to give conceptual sense, as expected and discussed earlier. In the present cases, grouping species by conformity testing likewise failed to give meaningful conclusions. This was because dividing the sites into groups reduced the populations of most species to levels below those at which differences were outstanding. The time-groups were distinguished by summations of tendencies which when considered individually revealed little.

SERIES II (48 sites, 2 times)

QUADRATS \times TIMES DATA

These are only considered in relation to site-groups and time-groups and are detailed later.

SPECIES \times QUADRATS DATA

SITE-GROUPS: The dendrograms of site-groupings (Fig. 13) gives an initial dichotomy; the site-groups so obtained lie offshore and onshore respectively. To obtain the maximum number of conforming species required more homogeneous site-groups; eventually seven major groups were adopted as shown on the dendrogram base. This left two isolated sites, 27 and 14; the former was allocated to the major site-group with greatest biotic affinities, site-group E. Site 14 is very dissimilar from the remainder, due to large numbers of species 2 (*Mesochaetopterus minutus*) and was retained as an isolate. The site-groups thus adopted are map-plotted on Fig. 14.

Site-groups A, B and C, which are tolerably closely linked in the dendrogram, all comprise inshore sites. Group A is the most inshore, B is intermediate and western, C is the deepest of the three and eastern. Site-group G, by dendrogram more distantly related to the above three groups lies nearest to the river mouth and tends to be more offshore than site-group C.

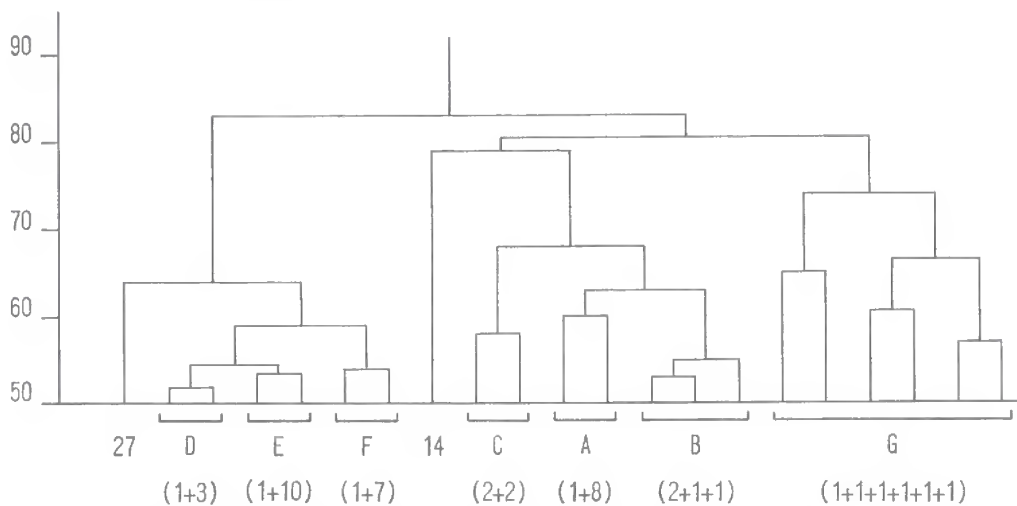


FIG. 13: Series II data (48 sites); truncated dendrogram of classification of sites by species; number of sites in each group in parenthesis at dendrogram base.

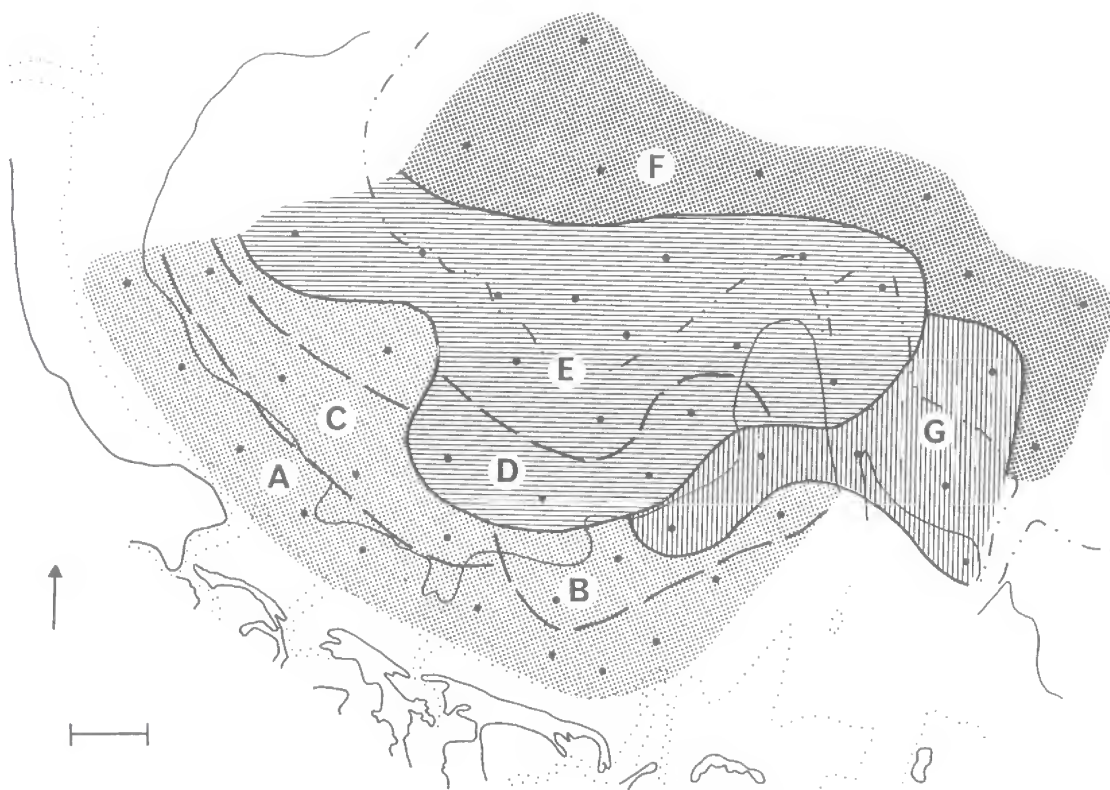


FIG. 14: Site-groups: 48 sites, classified by species after re-allocation of site 27. Scale line = 1 km.

Site-groups D, E and F are closely linked in the dendrogram, especially D and E. Topographically the three form a series with D closest inshore, E intermediate and F offshore. Site-group F extends laterally to off the mouth of the Brisbane River.

In general there is a clear topographic pattern, in which the most obvious relationship is to depth/distance offshore. The separation of site-group G seems to indicate a second influence, that of river proximity.

SPECIES-GROUPS: Apart from three isolated species (2, 45, 46) there is almost a trichotomy into three groups. By further division of the larger groups seven major species-groups were obtained (Fig. 15).

F tests were performed to determine which species had noticeably different values in the seven site-groups. Only 30 out of the 69 species in the analysis conformed, i.e. 43% compared with 67% in the series I data.

This is not because there are now more 'patchy' species concentrated in a single site. There are seven such species; these, with sites of occurrence in parenthesis, are: 2(14), 6(48), 20(45), 37(31), 40(48), 45(47), 46(47). The difference is due to the fact that there are many more 'random' species. This is a reflection of the lower recordings; present data involve four grab catches, while the series I data involved fourteen.

Perusal of the two-way table revealed that in several species-groups there was uniform or nearly uniform positive characterisation of a site-group by a species-group. Species-group I showed concentration in site-group A, (extreme inshore) except for one species (41) with a single outstandingly high value outside the area; species-group IV characterised site-group E; species-group VI showed major concentration in site-group G (near river mouth) and minor concentration in site-group D (adjacent). Species-groups V and VII comprised species with low recordings mostly approximating to random scatter amongst the sites, and there remains species-group III, the largest of all. The most discrete sub-unit comprises species 4, 5, 7, 12, 27, 31 and 38, and these are concentrated in site-group E. The remainder do not consistently characterise any of the site-groups. Perusal of the data suggests that the remaining eleven species (9, 13, 14, 21, 22, 24, 26, 29, 32, 35, 43) characterise an alternative grouping of sites, with concentrations in an area approximately encompassing sites 6, 11, 12, 13, 17, 19, 20, 21, 22, 23, 24, 25, and 26.

FEATURES OF THE SITE-GROUPS: A condensed 2-way coincidence table (Table 6A) summarises the site-group/species-group relationships as regards the commoner species. Perusal of the equivalent table for the series I data (Table 3A) shows many differences; both site-groups and characterising

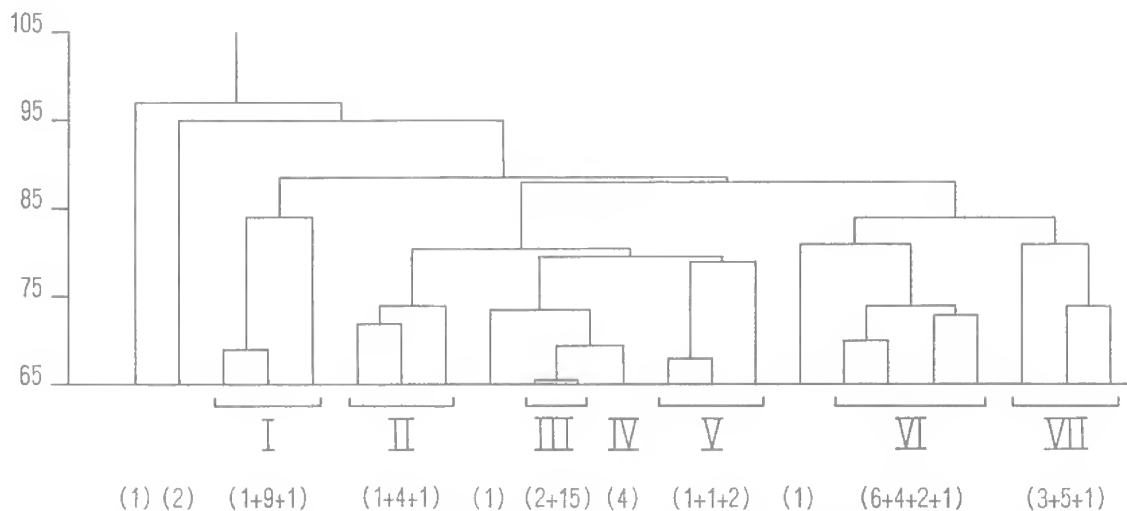


FIG. 15: Series II data; truncated dendrogram of classification of species by sites. At base species-group numbers used in text, and in parenthesis number of species in each.

TABLE 6: SERIES II DATA (48 SITES); SPECIES \times SITESA. MEAN NUMBER OF SPECIMENS/m² OF MORE ABUNDANT SPECIES IN MAIN SITE-GROUPS

Species group	Species and code No.	Main site-groups (sites in parenthesis)						
		A (1-6, 35-37)	B (8, 9, 34, 38)	C (7, 10, 13, 15)	D (11, 12, 17, 19)	E (20 27, 33)	F (28, 32 42, 43)	G (16, 18, 45-48)
I	<i>Spisula</i> , 1	2626	261	1	0	<1	0	0
	<i>Xenophthalmus</i> , 3	228	3	10	3	6	0	42
	<i>Amphitrite</i> , 10	27	5	0	0	0	0	0
II	<i>Amphioplus</i> sp., 6	0	2	1	4	5	55	9
	<i>Parcanassa</i> , 15	0	0	0	0	2	14	1
III	<i>Paratapes</i> , 4	1	6	10	53	133	58	2
	<i>Anadara</i> , 5	0	1	2	6	31	57	1
	<i>Amphioplus lobatus</i> , 7	0	0	5	12	31	8	0
	<i>Terebellides</i> , 9	8	4	19	22	15	5	0
IV	<i>Pupa</i> , 11	1	5	3	0	15	0	6
VI	<i>Theora lata</i> , 8	2	5	6	22	1	0	53
	tunicate 1, 18	0	3	2	12	0	0	10

*Mean number of specimens per sample, converted to numbers/m² and rounded to nearest unit.

B. MEAN POPULATIONS AND MEAN INDIVIDUAL SHANNON DIVERSITIES* IN TIME-GROUPS

I	Main site-groups						
	A	B	C	D	E	F	G
Mean N/m^2	2946	361	109	218	332	242	267
Mean H^1	0.42	0.66	1.05	0.92	0.82	0.67	0.81

*Meaned from values per sample of two 0.1 m² grab catches.

species-groups have changed and this makes detailed comparisons difficult. If a choice is to be made between the species/site results of the two studies, that from the more extensive series I data is preferred.

Of the abiotic factors which might influence the series II site-groups, sediment relationships are obscure (compare Figs. 3 and 4 with Fig. 14); an effect of the Brisbane River is clear; but the main factor appears to be related to distance offshore. Whether this is due to depth, dilution, turbidity, or some other factor is unknown.

Table 6B shows population densities and mean individual diversities within the site-groups, and as before there is an inverse relationship. Again the most inshore group (site-group A) has the highest populations. The groups at intermediate depths differ from each other as regards population density and diversity: lowest populations and highest diversities are in the central somewhat inshore site-group C; site-group G nearest the Brisbane River has roughly average values for both; and the most offshore site-group F has somewhat lower populations and higher diversity than average.

SPECIES \times TIMES DATA

With only two times, the times classification is a single dichotomy. This is at a dissimilarity level of 21%, considerably less than the dissimilarity between the two Septembers based only on 27 sites (31%). The decrease is due to the inclusion of sites which are more offshore and/or further from the Brisbane River.

With only two times, there is no variability of species-in-times, and the F test cannot be employed. Use of the χ^2 test on raw numbers (summed over all sites) showed 22 species with higher populations in 1972, 18 with higher values in 1973, leaving 39 without noticeable differences.

Total populations of all species summated were lower in time 1 with an average of 408 individuals/m² compared with 1346 in time 2. Mean individual diversities were 0.74 and 0.67 respectively.

DISCUSSION

This involves three main topics, (a) methods, both sampling and numerical, (b) matters related to airport construction, and (c) general matters related to communities, productivity, etc.

METHODS

SAMPLING METHODS: Stephenson, Williams and Cook (1974), established certain desiderata based on their work at Peel Island which could not be followed in the present study. These were that stations should be c. 0.25 km apart and that there should be quintuplicate grab catches on each occasion. In the present work samples were c. 1 km apart and catches were in duplicate.

The results obtained have in general shown that the wider spacing of sites was acceptable in that the site-patterns obtained have been topographically coherent and meaningful. Only one site (14) has not been closely linked to its neighbours and this was due to patchy distribution of species 2 (*Meso-chaetopterus minutus*).

Nevertheless problems remain over the spacing of sites. On each sampling two catches were made in close proximity but on a subsequent occasion the pair were likely to be up to 25 m from the originals. If a species is patchily distributed then on one occasion it might be collected and on another missed. In brief, microtopographic patterning could give the appearance of a marked seasonal change in numbers. A sufficient number of species showed 'saw-tooth' types of seasonal change to suggest that this was occurring. This casts doubts on the reality of the supposed time changes of the remaining species. Nevertheless a sufficient number of species give 'sensible' results for the time changes described to be regarded as real.

Further evidence for this was obtained by analysis of time-changes within sub-units of the sampling area. Here the data are weaker because summations involve fewer sites, but the time analyses result in somewhat greater conceptual sense.

NUMERICAL METHODS: Apart from a paper written after but published before the present account (Stephenson and Dredge 1975) the last published account of classifying multidimensional data which we are aware of was by Stephenson, Williams and Cook (1974). This involved variance measures of dissimilarity, whose magnitudes are very sensitive to the type of data transformation which is used; also it failed to give optimal species-groupings.

Since this, work experience has been gained in a variety of analyses of two-dimensional data by the senior author in concert with other workers. These include unpublished work by Godfriaux and Stephenson, preliminary reports upon the present work by Raphael and Stephenson (1972), and manuscript work by Stephenson *et al.* on wastewater outfalls at Los Angeles. Throughout, this

work has shown that for benthic analyses the Bray-Curtis measure of dissimilarity has advantages. Used on raw data dissimilarities are possibly too strongly biased towards the numerically abundant species and it is generally desirable to use transformed data. In the earlier work quoted above (Godfriaux and Stephenson, Raphael and Stephenson) the \sqrt{n} transformed was used, and this was also employed by Raphael (1974) in her thesis. Stephenson *et al.* (in MS) used the cube root transformation with the Bray-Curtis measure, but in the present work the more stringent $\log(n+1)$ transformation has been employed. It follows precedents created by Field and Robb (1970), Day, Field and Montgomery (1971), Field and Macfarlane (1968), Field (1971) and Christie (1974). However the choice was mostly influenced by results not yet published concerning the effects of a major flood on the present biota.

Following Boesch (personal communication), the preliminaries to the present work, and the manuscript work by Stephenson *et al.* for species-groupings we have used the proportionality of a species-in-sites instead of the absolute recordings. (Actually the proportions of transformed values were used.) This has resulted in better groupings of species with similar site recordings and has been an improvement compared with the variance technique of Williams and Stephenson (1973), and of Stephenson, Williams and Cook (1974). Meanwhile from a more theoretical aspect Dale and Anderson (1973) have already shown that optimal groupings of sites and of species do require different techniques.

In the present method as in the original 3D treatment of Williams and Stephenson (1973) we summed along a specified axis of the matrix to produce three two-dimensional matrices of $q \times t$, $s \times q$, and $s \times t$ respectively. As a consequence in each matrix variability in the other axis is lost and a single large recording of a species in a sample can influence all three of the two-dimensional matrices. A technique has been developed to locate and 'give warning' of such single outstanding values. It involves an *F* test (on transformed data) in which the largest value is compared with the remainder. In the present work 'patchy' species were also sought by heuristic examination of the results of site analyses and of time analyses. There was general agreement between the test and the conclusions drawn from site analyses.

In one respect the present methods revert to those of Stephenson, Williams and Cook (1974). This is in the use of the *F* test for investigating the conformity of species to entity-groups (i.e. site-groups or time-groups). We appreciate that the

data to be tested have been grouped by near-optimal techniques and that the basis for testing of significance is hence destroyed. However we suggest that this test still has conceptual value and has a close relationship to the intuitive bases of data scanning. Because it takes more strict account of within-group variation, it seems preferable over other tests. Throughout it was used at different levels in the classificatory hierarchies, and the levels finally selected gave the maximum number of conforming species.

Although the present methods have proved generally satisfactory, problems remain over species-groups; species within a group sometimes fail to conform in a uniform way to the entity groups. In some cases this has proved conceptually helpful as indicating alternative site-groupings. Such groupings have been sought unsuccessfully in two previous studies (Stephenson, Williams and Cook 1974, Stephenson *et al.* in MS).

In general species-grouping using sites data has proved satisfactory, but species-grouping with times data has not. The problems have been discussed earlier and have been partially resolved in the present paper by intuitively based analyses. As yet these defy formalization to the level of computer programming.

RELATION TO AIRPORT CONSTRUCTION

To predict changes in the Bramble Bay benthos due to airport construction requires (1) that there should be recognisable and quantifiable patterns in the biota before construction, (2) an estimation of which patterns are likely to change due to overall human activities, and (3) estimation of the particular effect of airport construction.

Site-patterns have been obtained with both the series I data (27 sites, 7 times) and the series II data (48 sites, 2 times). As might be expected these are not identical, but they do show broadly similar tendencies. It is of especial interest that the boundaries of the middle-depth site-groupings bulge shorewards opposite Serpentine Creek. For this there are two possible explanations, either a specific effect of Serpentine Creek, or the fact that it is an area roughly midway between two larger systems of freshwater drainage. Whichever is involved, the reduction in run-off from Serpentine Creek following airport construction is likely to cause changes. Present data show the area has relatively high diversity but relatively low population density.

Only the series I data produced time patterns worthy of further consideration. These show that there are noteworthy time changes and that these

involve very little repetition from the seasons of one year to those of the next. Instead certain species characterise the total area for a certain period (e.g. 9 months) and are superseded by other species. Time changes are most marked in the area nearest the Brisbane River. They indicate an annual change-over in biota in the inshore sites and an approximately six-months change-over in the offshore sites. It was suggested that variable run off of freshwater was the major cause of these temporal changes and if this is so, occlusion of Serpentine Creek might lead to increased temporal stability. The general literature on biotic diversity suggests that this would result in an increase in diversity. However this is far from certain and the reverse might well be true (see Stephenson, Williams and Cook 1974; Clifford and Stephenson 1975).

It is clear that investigations of considerable duration, much in excess of the proposed two years, would be required before adequate predictions could be made concerning temporal changes during 'normal' conditions. The flood of January 1974 terminated such 'normality' and as will be shown in a later paper produced dramatic effects.

Airport construction will be only one of many human influences which will operate in the area. Other factors include:

- (a) Shell dredging. This currently occurs at site 5 and inshore of sites 6 and 14; it may well extend in the future.
- (b) Prawn trawling. This occurs seasonally throughout the area except for the inshore sites. Annual variations in trawling intensity in the area have not been adequately quantified.
- (c) Port construction. Major construction at Fisherman Island with filling of the Boat Passage seems probable. This is likely to cause marked changes in the suggested 'Brisbane River' effect.
- (d) Reduction of pollution. Industrial pollution of the Brisbane River and Cabbage Tree Creek is currently being reduced, and discharge of untreated sewage is likely to be reduced in the future.

Amidst the welter of probable changes due to man, and with the ever-present possibility of another devastating flood, predictions of the effects of airport construction can only be tentative.

GENERAL MATTERS

Most workers on benthic biotas still feel constrained to express their results in terms of benthic communities, although it has been shown that the

community concept is complex and possibly confusing (see Stephenson 1973; Clifford and Stephenson 1975). In the present case it is not possible to accept the restraints of Petersen (1914) and limit the species characterising the sites to those with constantly high populations. The populations of virtually all species show changes during the sampling periods.

By taking averages over all times, groups of sites characterised by groups of species can be revealed. In the 27 sites analysis the most important of these are: inshore a *Spisula-Xenophthalmus-Terebellides* group; in the middle a *Xenophthalmus-Anadara-Paratapes* group; and offshore a *Paratapes-Amphioplus lobatus* group. In the 48 sites analysis there is greater topographic resolution but characterization of site-groups by species-groups is less distinctive. The inshore species-group is now *Spisula-Xenophthalmus-Amphitrite* and the offshore area group is *Paratapes-Anadara-Amphioplus lobatus-Terebellides*. These "communities" bear scant relationship to that of the adjacent area of Moreton Bay in the dredge study by Stephenson, Williams and Lance (1970). The difference is mainly due to the different collecting methods, as already noted in the Peel Island study (Stephenson, Williams and Cook 1974). There is a somewhat closer relationship to the characterizing species which Hailstone (1972) noted in a dredge study of the lower Brisbane River. Hailstone obtained large numbers of *Spisula* with *Parcanassa* and other species in shallow sandy-mud sediments, while *Anadara* characterized mid-channel sites with muddy sand. MacIntyre (1959) in his study of Lake Macquarie in New South Wales also obtained large numbers of several of the present species, particularly *Anadara*, *Paratapes*, and *Amphioplus lobatus*. Black (1971) noted that *Spisula* is common from sandy sites in Port Phillip Bay, Victoria, and it is listed from three regions in that bay by Poore and Rainer (1974). Other species of *Spisula* are well-known characterizing species elsewhere (see Thorson 1957) and a *Xenophthalmus* community is known from sandy grounds in the Persian Gulf (Thorson 1957).

Possibly the closest parallel with the present results is the New Guinea study by Stephenson and Williams (1971). Here there was an *Amphioplus* and a *Mesochaetopterus* 'community' both in a warm water situation under estuarine influence. The study by Stephenson, Williams and Cook (1974) is closest to the present work in times of sampling and analytical methods but the abundant species characterising site-groups have little in common.

Present results show that the densest populations are inshore, and the mean value for one data set is

1858 specimens/m² and for the other 2946. These values compare with 16–764 by Chukchin (1963) in eastern Mediterranean at depths of 100–200 m; 102–255 by Kuznetsom (1963) in the northern Pacific at depths to 500 m; 740–5515 by Wigley and McIntyre (1964) in the western North Atlantic at 40–366 m; and 32–1193 by Christie (1974) in South Africa at depths to 50 m. Values obtained by Sanders *et al.* (1965) were much higher (to 21263/m²) but they used a finer mesh sieve (0.42 mm). It is unfortunately not possible to compare present densities with those of the current extensive investigations in Port Phillip Bay, Victoria. Poore and Rainer (1974) deal only with molluscs and give an overall mean of 1457 individuals/m². This suggests that densities involving all species will be distinctly higher than those of the present study.

In the inshore sites, with the densest populations, it appears that there are marked annual changes in populations. This must result in high productivity of the benthic macrofauna; in absence of biomass determinations its magnitude is unknown. In the most offshore site-group in the 27 sites data, populations are lower and average 346 animals/m². Here however there are indications of a marked biotic change every six months. Again the macrofauna productivity must be of a high order.

Possibly the most interesting results of the present survey concern the time changes in biota. They confirm the opinion stated by Stephenson, Williams and Cook (1974) and by Clifford and Stephenson (1975) of the extremely doubtful value of many of the environmental impact statements involving benthic organisms.

The time investigations, cautiously interpreted because of possible microtopographical patterning, still stress the transitory nature of some of the species and the marked fluctuations in the populations of others. They give pointers to matters of both practical and fundamental importance. From a practical viewpoint, if environmental conditions are not too greatly disturbed, it appears that one biotic assemblance can readily replace another. It can hence be regarded as a buffered biotic system; provided airport construction does not greatly disturb conditions one might expect the buffering to operate tolerably quickly. Another and somewhat different aspect of 'buffering' in benthos has been noted in a recent paper involving a 4-year study by Buchanan, Kingston and Shearer (1974).

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APPENDIX

Species (and their systematic group) in order of abundance in all samples ($27 \times 7 + 21 \times 2$); only species occurring ≥ 9 times listed. Code number is given in first column and total population in last column.

1	<i>Spisula trigonella</i> (Lamarck)	Pelecypoda (Mactridae)	19318
2	<i>Mesochaetopterus minutus</i> Potts	Polychaeta (Chaetopteridae)	3367
3	<i>Xenophthalmus pinnotheroides</i> White	Decapoda (Pinnotheridae)	2457
4	<i>Paratapes scordalus</i> Iredale	Pelecypoda (Veneridae)	2238
5	<i>Anadara trapezia</i> Deshayes	Pelecypoda (Arcidae)	532
6	<i>Amphioplus</i> sp.	Echinodermata (Ophiuroidea)	520
7	<i>Amphioplus lobatus</i> (Ljungman)	Echinodermata (Ophiuroidea)	456
8	<i>Theora lata</i> Hinds	Pelecypoda (Tellinidae)	358
9	<i>Terebellides stroemi</i> Sars	Polychaeta (Terebellidae)	323
10	<i>Anphitrite rubra</i> (Risso)	Polychaeta (Terebellidae)	283
11	<i>Pupa fumata</i> (Reeve)	Gastropoda (Acteonidae)	221
12	<i>Theora</i> sp.	Pelecypoda (Tellinidae)	216
13	<i>Amphipholis loripes</i> Koehler	Echinodermata (Ophiuroidea)	204
14	<i>Leanira ytleni</i> Malmgren	Polychaeta (Aphroditidae)	199
15	<i>Parcanassa mangeloidea</i> Reeve	Gastropoda (Nassariidae)	185
16	<i>Lumbrineris latreilli</i> Audouin and Milne Edwards	Polychaeta (Eunicidae)	117
17	<i>Loimia medusa</i> (Savigny)	Polychaeta (Terebellidae)	108
18	tunicate 1	Ascidacea	105
19	tunicate 3	Ascidacea	101
20	bivalve 1	Pelecypoda	98
21	<i>Nucula astricta</i> Iredale	Pelecypoda (Nuculidae)	94
22	oyster 1	Pelecypoda (Ostreidae)	94
23	<i>Pectinaria antipoda</i> Schmarda	Polychaeta (Pectinariidae)	90
24	<i>Nereis jacksoni</i> Kinberg	Polychaeta (Nereidae)	90
25	<i>Mesochaetopterus</i> cf. <i>capensis</i> (McIntosh)	Polychaeta (Chaetopteridae)	90
26	<i>Ophelina gigantea</i> Rullier	Polychaeta (Opheliidae)	88
27	sea anemone 1	Actinaria	87
28	<i>Isolda pulchella</i> Müller	Polychaeta (Ampharetidae)	76
29	bivalve 2	Pelecypoda	74
30	<i>Tellina texturata</i> Sowerby	Pelecypoda (Tellinidae)	66
31	<i>Glycera prashadi</i> Fauvel	Polychaeta (Glyceridae)	62
32	<i>Cirrifornia</i> sp.	Polychaeta (Cirratulidae)	61
33	<i>Protankyra</i> sp.	Echinodermata (Holothuroidea)	61
34	<i>Petaloproctus terricola</i> Quatrefages	Polychaeta (Maldanidae)	55
35	bivalve 3	Pelecypoda	55
36	<i>Chama fibula</i> Reeve	Pelecypoda (Chamidae)	54
37	<i>Cycladicama</i> sp.	Pelecypoda (Ungulinidae)	53
38	balanid 1	Cirripedia	52
39	<i>Edwardsia</i> sp.	Actinaria	48
40	<i>Onuphis</i> sp.	Polychaeta (Eunicidae)	46
41	<i>Placamen sydneyense</i> Menke	Pelecypoda (Veneridae)	45
42	<i>Dasybranchus caducus</i> (Grube)*	Polychaeta (Capitellidae)	44
43	<i>Arca</i> sp. 1	Pelecypoda (Arcidae)	41
44	oyster 3	Pelecypoda (Ostreidae)	40
45	<i>Amphioplus depressus</i> (Ljungman)	Echinodermata (Ophiuroidea)	40
46	<i>Trichomya hirsuta</i> (Lamarck)	Pelecypoda (Mytilidae)	39
47	<i>Leptomya pura</i> Angus	Pelecypoda (Semelidae)	36
48	<i>Mesochaetopterus</i> sp.	Polychaeta (Chaetopteridae)	33

49	aphroditid 1	Polychaeta (Aphroditidae)	32
50	<i>Leonnates stephensoni</i> Rullier	Polychaeta (Nereidae)	31
51	<i>Clorida granti</i> (Stephenson)	Stomatopoda	30
52	<i>Marphysa sanguinea</i> (Montague)	Polychaeta (Eunicidae)	30
53	<i>Glossobalanus hedleyi</i> Hill	Enteropneusta (Balanoglossidae)	30
54	<i>Reticumassa paupera</i> Gould	Gastropoda (Nassariidae)	28
55	nemertean 'pink'	Nemertea	27
56	whip coral	Gorgonacea	27
57	<i>Venus</i> sp.	Pelecypoda (Veneridae)	26
58	<i>Macoma donaciformis</i> Deshayes	Pelecypoda (Tellinidae)	25
59	<i>Ophiactis perplexa</i> Koehler	Echinodermata (Ophiuroidae)	24
60	<i>Anomia</i> sp.	Pelecypoda (Anomiidae)	20
61	amphipod 4	Amphipoda	20
62	<i>Elaménopsis lineata</i> A. Milne Edwards	Decapoda (Hymenosomidae)	19
63	<i>Pista</i> sp.	Polychaeta (Terebellidae)	19
64	amphipod 2	Amphipoda	18
65	<i>Amacana trilobata</i> (Sars)	Polychaeta (Terebellidae)	18
66	<i>Hexapus granuliferus</i> Campbell and Stephenson	Decapoda (Goneplacidae)	18
67	tunicate 2	Ascidacea	16
68	<i>Chaetopterus variopedatus</i> Renier	Polychaeta (Chaetopteridae)	15
69	sabellid 1	Polychaeta (Sabellidae)	15
70	<i>Natica</i> sp.	Gastropoda (Naticidae)	14
71	amphipod 6	Amphipoda	14
72	<i>Tapes watlingi</i> Iredale	Pelecypoda (Veneridae)	13
73	amphipod 1	Amphipoda	12
74	<i>Bedeia hanleyi</i> Angus	Gastropoda (Muricidae)	12
75	<i>Brissoopsis luzonica</i> (Gray)	Echinodermata	12
76	nemertean 'black'	Nemertea	11
77	<i>Modiolus 'ostentatus'</i> Swainson	Pelecypoda (Mytilidae)	11
78	ampharetid 1	Polychaeta (Ampharetidae)	11
79	<i>Paplia subrugata</i> Iredale	Pelecypoda (Veneridae)	10
80	<i>Eurythoe parvecarunculata</i> Horst	Polychaeta (Amphinomidae)	10
81	<i>Polydora</i> sp. 1	Polychaeta (Spionidae)	10

*Possible misidentification.

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